

## Stumps as a habitat for Collembola during succession from clear-cuts to old-growth Douglas-fir forests

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**Summary.** We studied the natural succession of the collembolan fauna during the decomposition of stumps in successional Douglas-fir ecosystems at three sites on southern Vancouver Island, British Columbia, Canada. Each site was represented by four seres, comprising regeneration (3–8 years old), immature (25–45 years old), mature (65–85 years old), and old growth stands (>200 years old). A total of 216 samples collected during autumn, winter and spring yielded 15601 individuals, comprising 72 species, 40 genera and 12 families. Most of the species encountered (63.8%) were common to all sites. Densities on a volume basis equaled those in soil. Well-decayed stumps contained about 850000 individuals m<sup>-3</sup>. This species-rich and numerically abundant collembolan fauna was essentially a subset of the soil fauna. The composition of the collembolan community was more sensitive to the successional status of the forest than to season of sampling or to decay status of the wood. Stumps provided a suitable habitat for most soil Collembola and emphasizes the importance of this woody debris in forest ecosystems. Favourable moisture conditions make this habitat an important refugium for these arthropods during early stages of forest succession. By virtue of the large population in stumps, Collembola likely contribute greatly to the decomposition of this woody material.

**Key words:** Soil fauna, biodiversity, decomposition, coarse woody debris, forestry practices

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### Introduction

The importance of coarse woody debris (CWD) as an essential component of terrestrial ecosystems has been recognized only recently (O'Neill et al. 1975; Reichle et al. 1975; Harmon et al. 1986). Logs account for most of the CWD input in virgin North American coastal forests, but in second-growth and subsequent forests, stumps may form the major part of CWD in the forest floor (Harmon et al. 1986).

Stumps provide an array of ecological functions. They supply organic material to soil (Ausmus 1977), help to retain moisture (Harvey et al. 1978), are primary sites for nitrogen-fixation (Jurgenson et al. 1977) and the substratum for ectomycorrhizal activity (Harvey et al. 1979), and act as "nurse beds" for crop trees (McKee et al. 1982). Stumps also provide a habitat for many terrestrial vertebrates and vast numbers of invertebrates (Kühnelt 1976). The importance of this fauna in wood decomposition is well documented in Central Europe (Kühnelt 1976; Ausmus 1977), but has received little attention in North

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America, where effort has been directed mainly to log decomposition (see Harmon et al. 1986) and the insect fauna therein (Deyrup 1975, 1976, 1981). Analysis at the microarthropod species level has been lacking.

Intensive forest management dramatically alters the physical nature of forests, suggesting a reduction in biological diversity (Boyle 1991). Many invertebrate taxa, especially those with multiannual life cycles, require a series of logs and stumps at different decomposition stages to maintain stable populations. These invertebrate taxa could suffer from the decreased complexity characterized by managed forest (Ehnström 1984; Ishikawa & Ishikawa 1990). The complexity of managed forests is further reduced by practices of monoculture, whole-tree logging, slash burning and de-stumping. The reduced soil-fauna diversity could be reflected in a slower decomposition rate of CWD remaining on the forest floor and affect the productivity and sustainability of managed stands (O'Neill et al. 1975; Setälä & Huhta 1990). A simplified community of wood inhabiting fauna may act poorly as a "biocontrolling" system against various pests and diseases, which might benefit from the absence of potential predators to reduce pests and fauna to consume pathogenic bacteria and fungi (see Marshall 1993a).

In this study, we posed two questions: (i) what is the natural succession of the collembolan fauna during the decomposition of stumps in old-growth and managed Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco.) forests? (ii) How do changes in the abiotic environment resulting from clear-cutting affect the collembola succession? Douglas-fir ecosystems were selected because only small remnants of old-growth stands remain — and are in danger of disappearing — on southern Vancouver Island. It is important to know whether stumps provide refugia for soil fauna and contribute to the conservation of forest biodiversity. The Collembola were chosen, because, among the North American soil fauna, their taxonomy is relatively well known (Behan-Pelletier & Bissett 1992). The collembolan component is one of several studies being undertaken to document changes wrought by the conversion of old-growth to second-growth Douglas-fir forests (Marshall 1993b).

## Materials and Methods

### Site description

The three study sites are located on the southeastern part of Vancouver Island (Fig. 1). The sites are in the Coastal Western Hemlock Zone, Very Dry Subzone, in an area bordering the Coastal Douglas-fir Zone (Klinka et al. 1991). The stands are composed mainly of Douglas-fir with significant components of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and minor components of western red-cedar (*Thuja plicata* Donn), western white pine (*Pinus monticola* Dougl.) and red alder (*Alnus rubra* Bong.). Klinka et al. (1991) provided some climatic data and characterized the area as having mild temperatures throughout the year; the mean annual temperature being 9.3 °C and mean annual precipitation 1505 mm. Most of the precipitation at these three sites occurs as rain during the cooler winter months (Hare & Thomas 1979). Site 1 is in the Greater Victoria Watershed (48° 34' N; 123° 39' W) at an elevation of 308 m. Site 2 is mostly in this watershed but includes plots just outside its northern boundary (48° 38' N; 123° 43' W) and at an elevation of 383 m. Site 3, located more northerly (48° 39' N; 123° 46' W) and at a slightly higher elevation (594 m) than Sites 1 and 2, is characterized by a lower mean annual temperature (5.7 °C) and a higher mean annual precipitation (2349 mm). Each site contained stands with four "seral communities" according to successional age of the forest stand. Within each sere, an experimental plot (approximately 1 ha) was selected. The regeneration (REG) or clear-cut seres [Plots 3, 11, 21 in Trofymow and Blackwell (1993)] were 3–8 years old and supported young plantations of Douglas-fir, less than 1 m tall, and many understory species and pioneer plants characteristic of early succession. The immature (IMM) seres [Plots 5, 12, 22 in Trofymow and Blackwell (1993)] were 25–45 years old and supported young stands of Douglas-fir with minor components of other tree species as mentioned above. The mature (MAT) seres [Plots 6, 14, 22 in Trofymow and Blackwell (1993)] were 65–85 years old and supported a similar tree composition as the IMM seres. The old growth (OLG) seres [Plots 8, 15, 24 in Trofymow and Blackwell (1993)] were >200 years old and tended to have a greater component of western hemlock in the overstory.

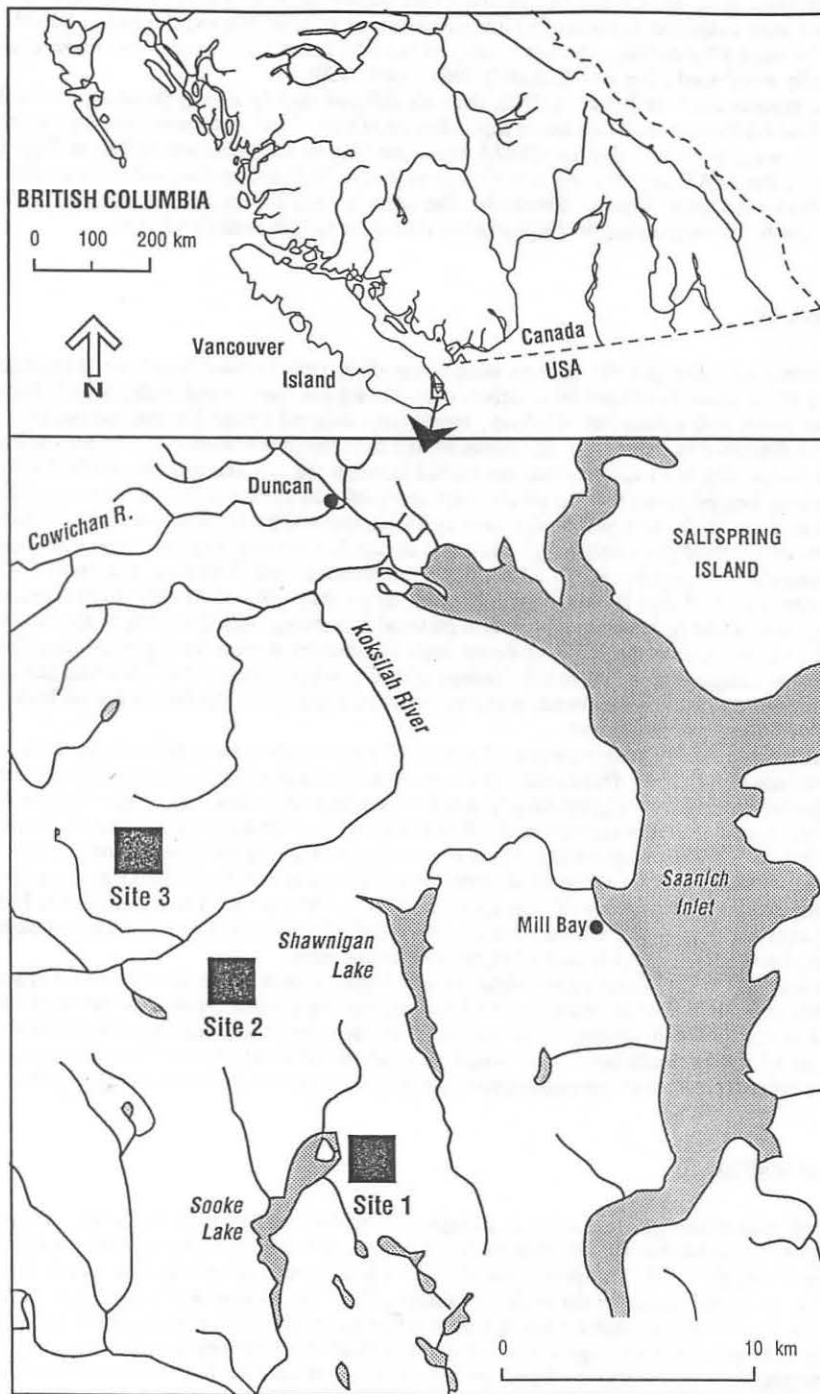


Fig. 1. Location of the three study sites on Vancouver Island, western Canada

Management practices, such as fertilization, thinning and pesticides, were not applied to these sites. However, all sites were subjected to forest fire during some part of their history: the REG and IMM seres were slash-burned after cutting; the fire history of the MAT and OLG seres is not known, but such stands usually developed after fire (Schmidt 1960; Agee 1990).

According to the classification of Jungen (1985), the soils differed slightly among the seres. At Site 1, the REG, IMM, and OLG seres were located on rapid-draining Orthic Dystric Brunisols [see Agriculture Canada Expert Committee on Soil Survey (1987)], corresponding to Dystrochrepts (USA) or Dystric Cambisols (FAO); the MAT sere was on a well-drained Duric Dystric Brunisol. All seres at Site 2 were on rapid-draining Orthic Dystric Brunisols. The seres at Site 3 were on well-drained Orthic Humo-Ferric Podzols, corresponding to Haplorthods (USA) or Orthic Podzols (FAO).

### *Stump classification*

In each successional sere Douglas-fir stumps were categorized into 3 decay stages using methods slightly modified from those described by Lambert et al. (1980) for logs: sound stump-wood (decay stage I), a sharp metal rod penetrates <0.5 cm; moderately decayed (stage II), the rod penetrates 0.5 cm to half the diameter of the stump, the sapwood and heartwood breaks into blocky pieces; and advanced decay (stage III), the rod can easily be pushed through the soft and powdery wood. Unlike logs, in which decay begins along the top of the bole and gradually proceeds deeper, decomposition of stumps tend to start at the top and at the base and subterranean parts simultaneously (Kühnelt 1976). Therefore, the method gives only rough estimates on the decay status of stumps when compared to logs. Consequently, our decay stage II of stumps approximates stage 3 of logs, and stage III of stumps equals stages 4–5 of logs (Sollins 1982). Usually, decay stages II and III were further verified according to the proportion of loose, mushy, wood material in a stump: less than 25% of the volume of this material in a stump was classified as decay stage II, whereas stumps having more than 75% of this material was categorized as stage III. Stumps of decay stage I always had bark and phloem tightly to moderately attached to the wood, whereas the more advanced stages had either no bark or only fragments of outer bark remaining.

Stumps originated from two sources: cutting of trees and natural tree-break, which happens today even in managed stands, especially from fungal diseases. Apart from clear-felling, stumps also resulted from earlier selective cutting (or "highgrading"), which was practiced in these coastal forests over the past century. The majority of the stumps in the REG seres were at decay stage I, being 6, 7 and 6 years old for sites 1, 2 and 3, respectively. Most stumps in the IMM seres were at decay stage II, being 58, 64 and 43 years old for these same three sites. Stumps in MAT and OLG seres resulted from highgrading and natural causes and their ages could not be determined. The stumps in the REG seres were fully exposed to sunlight, whereas those in the IMM, MAT and OLG seres, because of closed canopies, received less solar radiation and decayed at different rates.

Stump volume was determined from mean diameter and height of each stump in a 60 m × 30 m area in each plot. No adjustments were made for buttressing, and an average height was estimated for decay stage III stumps, which tended to be conical. On each sampling occasion, the gravimetric moisture content of a representative wood sample was calculated as a percent of wood dry mass. This sample was taken from each stump and approximated the volume of wood for faunal extraction.

### *Collembolan sampling*

The sampling of microarthropod densities in stumps was carried out on three occasions; in a dry, warm period (late September/early October 1991), in a cool, wet period (January 1992), and in a mild, wet period (April 1992). Samples from decay stage I stumps were taken as wood blocks (10 × 10 × 10 cm, excluding outer bark) with a chainsaw. Only one sample was taken from stage I stumps. Samples from stages II and III stumps were taken differently. A metal soil corer (diameter 5 cm) was pushed horizontally through the wood to a depth of 5 cm. Woody material was collected from three separate areas of the stump: from the top, middle, and near the bottom. Where available, two stumps from each decay stage per sere were selected randomly. These were separated at least 15 m from each other to minimize possible clustering of collembolan species.

In the laboratory, the wood blocks from decay stage I samples were chiseled into 1 cm-sections for extraction. One third of the samples taken from the 3 vertical layers of each stump of decay stage II was pooled to form one composite sample for extraction. A similar pooling of the three layers of

samples for extraction was done for decay stage III stumps. The microarthropods were extracted into picric acid with a modified high-gradient extractor (Lussenhop 1971) for one week. Temperatures in the extractor were controlled by data loggers. Morphologically similar collembolan specimens were sorted under a dissecting microscope, and representative specimens were mounted on microscopic slides for examination with a phase contrast microscope. Collembolan species were determined using keys from Christiansen & Bellinger (1980–1981). Family and generic placement did not always follow these authors, because of acceptance of different concepts in collembolan taxonomy. Voucher specimens have been deposited in the Soil Zoology Laboratory, Pacific Forestry Centre, Victoria, British Columbia.

### Data analysis

Several approaches were employed for analyzing the collembolan fauna from stumps with respect to the successional seres and different decay stages of the stumps. PC-ORD computer programs (McCune 1991) were used to assess the dissimilarity of the collembolan composition between and within seres. Because of the "multivariate nature" of the data set, multivariate techniques were used to reduce the amount of variation in community composition to the scatter of samples in the ordination diagram. Within the PC-ORD program, detrended correspondence analysis (DCA) (Hill & Gauch 1980) was used to test the distinctiveness of the collembolan fauna within and between sites, seres, and stump decay stages. DCA is an "eigenvector" technique that ordinales both species and samples simultaneously in a multidimensional biplot. A Multi-Response Permutation Procedure (MRPP) in the PC-ORD program was used to test the null hypothesis between groups of entities in the biplot. Renkonen's percentage similarity index (Renkonen 1938) and Morisita's similarity index (Morisita 1959) were also applied as reference tests for DCA. When population differences were tested by analysis of variance (ANOVA), a logarithmic transformation was used:  $x = \log_{10}(x + 1)$ , where  $x$  was the actual count of individuals. The level of significance was set at  $\alpha = 0.05$ . Tukey's test was used to separate significant differences among means for site, seres and seasons.

## Results

### Stump distribution and characteristics

Total stump volume and gravimetric moisture content, in each sere, are presented in Table 1. Stumps of decay stage I were numerous in the REG sere, but very limited in other seres.

**Table 1.** Characteristics of stumps of the three decay stages (I, II and III) in the four successional seres (regeneration, immature, mature, old growth); data are pooled for three sites. Volume =  $\text{m}^3 \text{ha}^{-1}$ ; data are pooled for all seasons. Moisture content = % water of dry mass; standard deviations are given in brackets below the moisture content values

	REG			IMM			MAT			OLG		
	Sep./ Oct.	Jan.	Apr.	Sep./ Oct.	Jan.	Apr.	Sep./ Oct.	Jan.	Apr.	Sep./ Oct.	Jan.	Apr.
Volume												
I		7.18 ± 1.93			0.27 ± 0.04			0.07 ± 0.11			0.40 ± 0.47	
II		0.24 ± 0.08			6.30 ± 0.48			1.24 ± 1.14			2.41 ± 1.07	
III		0.11 ± 0.15			0.97 ± 0.93			0.16 ± 0.08			0.41 ± 0.11	
Moisture												
I	62.2 (7.3)	118.3 (41.7)	135.3 (49.3)	121.9 (91.1)	— (—)	— (—)	144.5 (44.6)	266.6 (—)	123.9 (—)	129.6 (25.7)	83.9 (37.3)	105.7 (15.7)
II	102.5 (2.4)	172.3 (50.2)	170.9 (22.3)	198.5 (5.9)	234.0 (48.8)	202.7 (82.8)	149.0 (84.3)	210.9 (119.4)	243.0 (113.9)	170.3 (128.0)	221.5 (58.4)	140.8 (22.1)
III	71.2 (16.0)	233.0 (66.9)	175.8 (88.8)	193.8 (5.7)	209.9 (44.9)	161.7 (28.4)	205.3 (117.3)	206.5 (70.9)	207.7 (113.8)	136.6 (13.6)	161.0 (52.9)	152.3 (36.1)

Because of this, statistical analyses excluded data involving stumps of decay stage I. Stumps of decay stages II and III were sufficiently represented in all seres, although decay stage III stumps were found in smaller numbers. All stumps contained a comparatively high amount of water at all sampling times. However, there was a tendency for moisture to increase with advancing stages of decomposition. Also, stumps in the REG sere, in September, tended to be drier than those in the forested seres. There was however no correlation between stump moisture and collembolan abundance.

#### *General description of the collembolan fauna*

*Site effect:* The collembolan species collected from all stumps are listed in the Appendix. A total of 72 species, distributed among 40 genera and 12 families were identified from the 216 samples collected during the study, covering all sites, successional seres and decay stages of stumps. Most of the species encountered (63.8%) were common to all sites, and none of the sites harboured significantly more species or specimens than the others (Table 2). On this basis the 3 sites can be considered as true replicates in this study.

*Sampling time:* No significant differences in the structure of collembolan fauna were observed between samples collected in September/October, January, and April. Even when all data are pooled on the basis of the sampling time to form 3 composite samples, ANOVA did not show significant differences in the species number ( $P = 0.08$ ) or the individual abundance ( $P = 0.863$ ) between the sampling times. However, a pairwise comparison showed the total number of species in January ( $40.8 \pm 1.5$ ) to be significantly greater ( $P = 0.02$ ) than in April ( $32.0 \pm 3.2$ ), but not different than in September ( $37.50 \pm 7.55$ ). Detrended Correspondence Analysis (DCA) of decay stage II and III stumps showed that

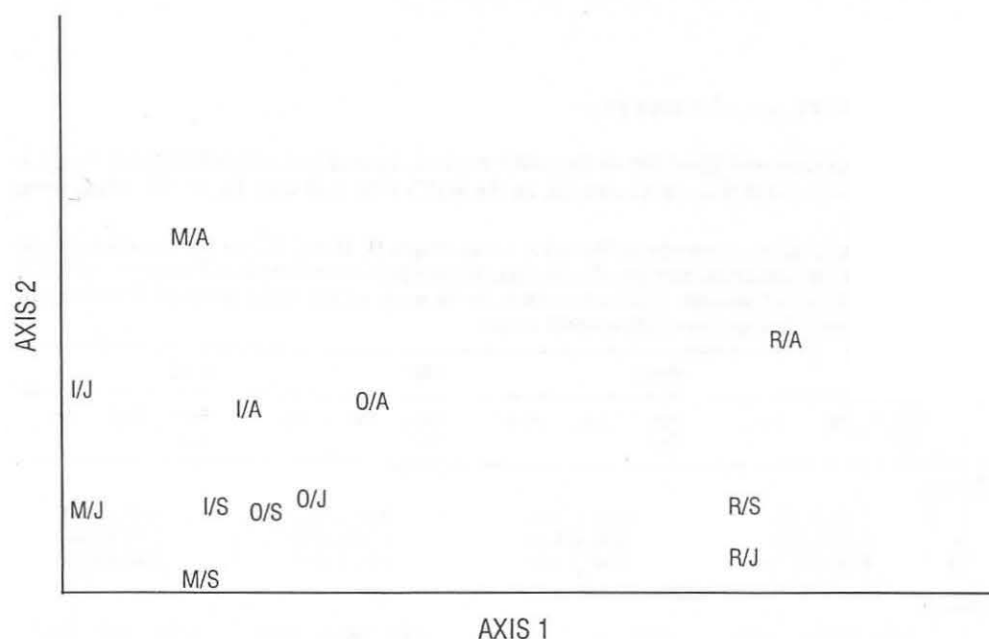


Fig. 2. Distribution of stump Collembola in a biplot with respect to sampling times (S = September/October, J = January, A = April), and successional ages of the Douglas-fir forest (R = regeneration, I = immature, M = mature, O = old growth) using detrended correspondence analysis (DCA). Data are pooled for decay stages II and III of stumps and for the 3 study sites



the age of the forest was more important than sampling time in clustering collembolan communities (Fig. 2). DCA graphically arranges entities (such as communities of organisms) so that similar entities are grouped closely together, and dissimilar ones are placed far apart. In the ordination, the communities did not group according to season of sampling, suggesting that there was no relationship between the distribution of the collembolan communities and season. However, some degree of clumping existed with respect to the sere in which the Collembola fauna was found, especially for the REG seres. In addition, MRPP showed that the probability was low ( $\Delta = 0.0408$ ) for forming entities that were more distinct than those based on stand age. No collembolan species was clearly restricted to any of the sampling times. Adults and immatures of many species were present on each occasion, suggesting that some of these species are multivoltine in stumps.

*Decay stages:* Apart from a few insect boreholes, decay stage I stumps were relatively unaltered, with the bark still well connected to the wood. Consequently, habitable space for Collembola in stage I stumps was much reduced compared to other decay stages. Therefore, collembolan communities in stumps of decay stage I likely differend from those found in stumps of more advanced decay status. On the total volume, the habitable space for Collembola in stumps of decay stage I occurred only at the interface between loose bark and sapwood (no bark was included in the samples). The efficiency of the extractor was not tested for wood, but we theorized that Collembola in decay stage I stumps would be present on wood surfaces or in boreholes that would allow them to exit during extraction. The very porous wood from decay stages II and III should allow the extraction of fauna in a manner not unlike litter. The species composition of decay stage II and III showed that the latter did not contain less vagile forms.

**Table 2.** Number of collembolan species in each sere (regeneration, immature, mature, old growth) in the three sites, mean number of individuals per sample ( $150\text{ cm}^3$ ) in stumps of decay stages II and III, and total number of species found per sere. Data are pooled for sampling times and decay stages of stumps

Sites	REG No. of		IMM No. of		MAT No. of		OLG No. of	
	Spp.	Indiv.	Spp.	Indiv.	Spp.	Indiv.	Spp.	Indiv.
1	32	34	37	119	41	80	45	76
2	34	72	38	128	40	164	39	115
3	30	50	31	119	39	134	33	140
Mean	32	52	35	122	40	126	39	110
Total No. spp. found per sere	46		49		54		54	

The community structure of the Collembola in decay stages II and III was somewhat different. The average number of species per sample did not differ significantly between these two decay stages ( $12.6 \pm 1.8$  and  $14.7 \pm 2.5$  in stage II and III, respectively), but the average number of collembolans per sample tended to be greater ( $P = 0.09$ , ANOVA) in stage III stumps ( $75.6 \pm 21.4$  in Stage II versus  $131.5 \pm 52.5$  in stage III). In addition, ordination analysis (DCA) showed a weak tendency for the collembolan fauna to be grouped according to the decay stage of a stump rather than successional age of seres. However, this was evident in the forested seres only;  $\Delta$  value of the MRPP = 0.0233. Only one collembolan species, the isotomid *Ballistura libra*, seemed to show a preference to a particular decay stage of stumps. It was generally more abundant and occurred more frequently in decay stage I stumps.

Table 3. Renkonen's and Morisita's (in parentheses) similarity indexes for collembolan communities of stumps in the four seres (regeneration, immature, mature, old growth). Data are pooled for sampling times and decay stages II and III stumps

	REG		IMM		MAT		OLG	
REG	100.0	(1.00)	51.9	(0.64)	54.0	(0.69)	58.6	(0.76)
IMM	—	—	100.0	(1.00)	83.6	(0.98)	79.9	(0.97)
MAT	—	—	—	—	100.0	(1.00)	82.4	(0.97)
OLG	—	—	—	—	—	—	100.0	(1.00)

#### Distribution in the successional seres

Collembolan numbers in the samples were highly variable both between and within seres. Therefore, the data from decay stages II and III were pooled for a single estimate for all seasons to compare the collembolan communities among different seres. This was considered appropriate since (1) large numbers of samples are required to obtain accurate estimates of microarthropod distribution (Macfadyen 1962); (2) the collembolan communities (both numbers of individuals and number of species) did not show major differences among stumps of decay stage II and III; and (3) the structure of the collembolan fauna remained similar at each sampling time.

With the pooled data, the four seres can be divided into two distinct groups with respect to the organization of the collembolan fauna in the stumps: the forested stands (IMM, MAT and OLG) and the clear-cut stand (REG). The number of individuals was significantly smaller ( $P = 0.001$ , ANOVA) in REG than in the forested seres (Table 2). Also, the average number of species in the stumps (decay stage II and III) in the REG were tended to be smaller than in the forested seres (Table 2). When expressed on a per sample basis (not per sere) the number of collembolan species in samples from the REG seres was significantly smaller ( $P < 0.05$ ) than in the other seres.

Table 4. Frequency (%) and abundance ranking of the most common collembolan species in the four seres (regeneration, immature, mature, old growth). Data are pooled for sampling times and decay stages II and III stumps

REGENERATION			IMMATURE		
	Freq. %	Abund. Rank.		Freq. %	Abund. Rank.
<i>Anurophorus septentrionalis</i>	80	II	<i>Folsomia</i> sp.	100	I
<i>Mesaphorura yosiii</i>	63	I	<i>? macroseta</i>		
<i>Folsomia</i> sp.	63	III	<i>Mesaphorura yosiii</i>	100	II
<i>? macroseta</i>			<i>Pogonognathellus flavescens</i>	78	VI
<i>Pseudisotoma sensibilis</i>	52	VIII	<i>Micranurida spirillifera</i>	78	X
<i>Pogonognathellus flavescens</i>	48	IX	<i>Pseudisotoma sensibilis</i>	72	V
<i>Ballistura libra</i>	37	IV	<i>Sminthurinus conchyliatus</i>	72	XII
<i>Hymenaphorura cocklei</i>	33	VI	<i>Hymenaphorura</i> sp.	67	III
<i>Pseudachorutes corticicolus</i>	26	XIII	<i>? talus</i>		
			<i>Desoria notabilis</i>	67	IV



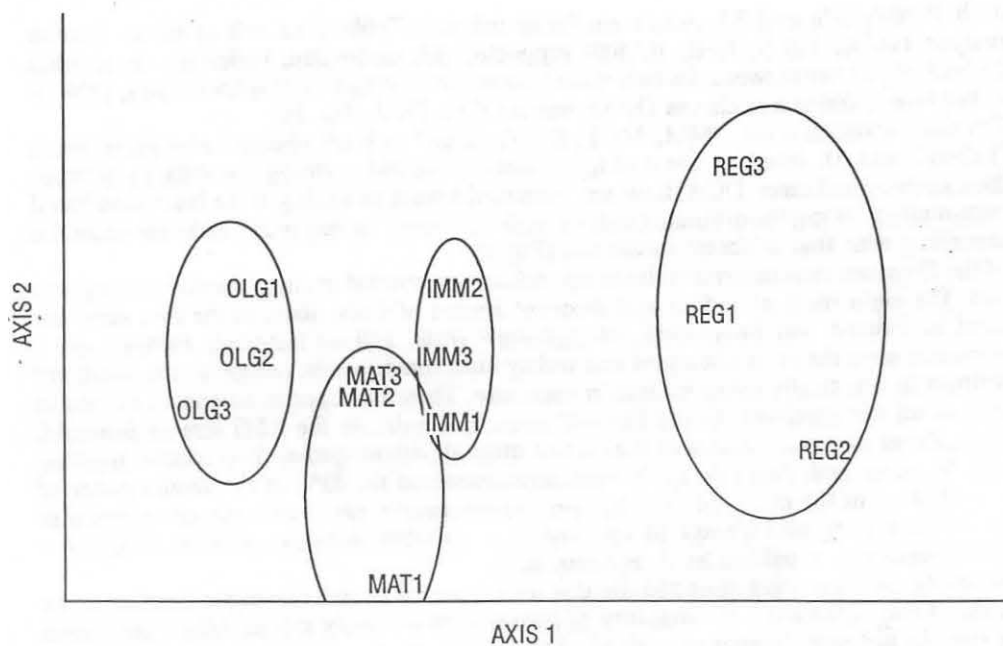


Fig. 3. Distribution of stump Collembola in a biplot with respect to study sites (1, 2 and 3) and successional ages of the Douglas-fir forest (REG = regeneration, IMM = immature, MAT = mature, OLG = old growth) using detrended correspondence analysis (DCA). Data are pooled for decay stages II and III of the stumps and for the 3 sampling times. Ellipses emphasize the grouping according to sères

MATURE			OLD GROWTH		
	Freq. %	Abund. Rank.		Freq. %	Abund. Rank.
<i>Folsomia</i> sp.	100	I	<i>Mesaphorura</i>	100	II
? <i>macroseta</i>			<i>yosiii</i>		
<i>Mesaphorura</i>	100	II	<i>Folsomia</i> sp.	94	I
<i>yosiii</i>			? <i>macroseta</i>		
<i>Micranurida</i>	72	IV	<i>Pseudisotoma</i>	89	IV
<i>spirillifera</i>			<i>sensibilis</i>		
<i>Pogonognathellus</i>	68	VIII	<i>Pogonognathellus</i>	84	VIII
<i>flavescens</i>			<i>flavescens</i>		
<i>Pseudisotoma</i>	61	VII	<i>Micranurida</i>	72	VII
<i>sensibilis</i>			<i>spirillifera</i>		
<i>Hymenaphorura</i> sp.	61	III	<i>Hymenaphorura</i>	72	III
? <i>talus</i>			<i>cocklei</i>		
<i>Friesea</i>	56	V	<i>Hymenaphorura</i> sp.	67	V
<i>millsi</i>			? <i>talus</i>		
<i>Sminthurinus</i>	50	XX	<i>Friesea</i>	61	VI
<i>conchyliatus</i>			<i>millsi</i>		

Both Renkonen's and Morisita's similarity indexes (Table 3) as well as the ordination analysis (DCA, Fig. 3; Delta 0.0500) supported this distinction, indicating the greatest dissimilarity either between the two earliest successional stages (Similarity indexes, Table 3) or between extreme age classes (REG versus OLG; DCA, Fig. 3).

The three forested seres (IMM, MAT, OLG) seemed to share similar collembolan fauna (Tables 2 and 3). None of the ecological indexes showed a strong dissimilarity between these successional seres. DCA, however, indicated a weak clustering of the fauna into "seral communities" along the ordinate (Axis 1), with "temporal" arrangement of the communities coinciding with that of forest succession (Fig. 3).

Of the 72 species encountered in this study, none was restricted to any particular successional sere. The eight most abundant and frequent species of Collembola in the four seres are listed in Table 4. An onychiurid, *Mesaphorura yosiii*, and an isotomid, *Folsomia* sp. ? *macroseta* were the most abundant and widely distributed species, occupying the dominant position in practically every sample in each sere. These two species accounted for about 60% of all the specimens in the forested seres. Generally, in the REG sere an isotomid, *Anurophorus septentrionalis*, was the second most abundant species. This species, together with *M. yosiii* and *Folsomia* sp. ? *macroseta* accounted for 52% of the total number of collembolans in the clear-cut. *Anurophorus septentrionalis* was found only occasionally in the forested seres and always in low numbers. Another isotomid, *B. libra*, followed a similar distribution pattern as *A. septentrionalis*.

Generally, only the eight most abundant species recorded in each sere had a high frequency (Table 4 and Appendix); the majority of species were accessory species, being uncommon or rare. Constancy (frequency > 50%) of these eight abundant species tended to increase with succession, giving four, eight, eight and ten species for REG, IMM, MAT and OLG, respectively. An average-size stump of decay stages II or III in a forested sere (61012 cm<sup>3</sup>; S.D. 45955) contained about 48800 specimens or about 799843 specimens m<sup>-3</sup>.

Following the classification of Wallwork (1970), the majority of the collembolan species from the stumps could be considered unspecialized feeders, consuming a variety of plant materials, bacteria, living prey, carrion and faeces. A few, especially in the Anurididae and Neanuridae, may not be able to ingest solid food, and *Hymenaphorura cocklei* was omnivorous, usually containing collembolan exuviae with other gut material. Throughout the study, the gut of the most dominant species, *Folsomia* sp. ? *macroseta*, contained mainly wood fragments, suggesting an important role in wood comminution by this collembolan species.

## Discussion

### *Stumps as a habitat*

Decaying stumps of Douglas-fir harbour a species-rich community with large numbers of collembolans (about 48800 specimens representing at least 15 species per stump). Since detailed information on microarthropod fauna of stumps in forests is lacking, comparisons are made here also with decaying logs. Values recorded here for both number of species and individuals are much higher than those previously reported for coarse woody debris. Wallace (1953) found 3 species of Collembola in decaying pine stumps in England, and Savely (1939) reported 6 species of Collembola from pine and oak logs in the Duke University forest, North Carolina, USA, but he did not accurately quantify their abundance. Fager's (1968) more extensive study, with invertebrates in decaying oak logs in England, listed 24 species of Collembola, but his total number of specimens was only about 10% of that in the present study. More recently, from central Oregon, Seastedt et al. (1989) compared the abundance and diversity of microarthropods in logs of several tree species to that in the soil. The density of Collembola was reported as 135000 individuals per m<sup>3</sup> of well decayed surface heartwood of Douglas-fir. This figure is only about a fifth of the density obtained in the present study.

A cubic meter of organic soil in an immature Douglas-fir forest contained about 770000 collembolans (Marshall 1974), whereas an equal volume of decay stage II/III stumps at the same location harboured approximately 800000 collembolans. So the population density of *Collembola* in both well decayed stumps and soil appear to be of the same magnitude. Unlike stumps, collembolan densities in logs might be much lower than the in soil, assuming the values of Seastedt et al. (1989) to be representative (135000 in logs versus 620000 individuals  $m^{-3}$  in soil).

The high density of collembolans in stumps may indicate the suitability of stumps as a habitat for other faunal groups. Although stumps consist of a fairly uniform substrate (mainly wood), compared to litter with soil, they nevertheless provide many niches even at the earliest stage of decomposition. Moisture is trapped in stumps as a result of the separation of bark from wood and the early invasion of wood-eating insects such as beetles and termites and tunnellers like phthiracarid mites. Favourable shelter and moisture regimes facilitated by early borers allow for the invasion of stump wood from the exterior by other soil fauna, including nematodes (H. Setälä & V. G. Marshall, unpublished). Conversely, the decomposition of logs, which tend to have intact bark adjacent to the soil; proceeds more slowly, starting from the upper surface only, thereby leaving heartwood relatively protected from faunal invasion for long periods (Harmon et al. 1986). The porosity of woody material increases with advancing decay (Sollins et al. 1987). Hence, the greater abundance of fauna in stumps of more advanced decay stages may also be a reflection of increased amounts of habitable space.

Although different kinds of coarse woody debris, including stumps, provide a well-defined habitat in an ecosystem, it may be difficult to consider this woody habitat as a separate "living entity" (i.e. with a unique fauna) sensu Shelford (1913), Graham (1925) and Savely (1939). Stumps may be a living entity for some insects and other macrofauna, but they do not seem to act in the same way for soil micro- and meso-fauna. Many animals move freely between soil and wood, particularly when unfavorable temperatures or scarcity of food and moisture make the litter an unsuitable habitat (Lloyd 1963). According to Seastedt et al. (1989), the microarthropod fauna of decaying wood could be considered a subset of the forest floor fauna, since few species, if any, are restricted to decaying logs only. Most of the species listed in the Appendix have been found in soil (references to species' habitat in Snow 1958; Salmon 1964–65; Christiansen and Bellinger 1980–81; Battigelli and Marshall 1993; K. Christiansen, pers. comm.; J. Rusek and V. G. Marshall, unpublished). Until now, *Sinella baca* and *Plutomurus wilkeyi* have been known only from caves and *Ballistura libra* and *Proisotoma beta* from moss. The occurrence of *Cheilotoma* sp. in stumps is not surprising as it is associated with termites, which inhabited many of the stumps. The following six species have been associated with stumps, wood or bark: *Friesia quinta*, *Pseudachorutes aureofasciatus*, *Pseudachorutes corticicolus*, *Pseudosotoma sensibilis*, *Sminthurinus conchyliatus* and *Vertagopus arborea*.

The collembolan communities in the stump samples were similar despite the clear structural dissimilarity of stump wood of different decay stages. This observation indicates a low degree of specialization of the *Collembola* for a particular microhabitat associated with stump decay stage. However, *Folsomia* sp. ? *macroseta*, the dominant species in stumps, occurs only rarely in soil samples near stumps, indicating that this species, and perhaps those associated with wood and bark already mentioned, might be specialized for woody habitats.

Seasonal changes in the structure of the collembolan fauna in this study were minimal as there was little indication of grouping of the collembolan fauna by time (Fig. 2). Marshall (1974) reported considerable seasonal fluctuation in *Collembola* numbers in LFH-layers of the same area, the minimum being in early winter and spring, and maximum in late summer. Sampling times of the present study coincided with the dates of Marshall's (1974) high and low abundances, but did not show the same temporal pattern. A lack of seasonal population oscillations was also observed in the clear-cuts with their more variable climate conditions. This indicates that the fauna do not exploit stumps purely as a shelter against unsuitable weather conditions, but as a preferred habitat throughout the year.

Stumps provide a distinctive habitat that is used by some vertebrates, for example salamanders (T. M. Davis, unpublished), and an array of invertebrates (Kühnelt 1976; Deyrup 1981; V. G. Marshall & H. Setälä, unpublished). Based on the lack of seasonal fluctuation, stump Collembola appear not to be a random assemblage of individuals but rather an organized stable community (sensu Grossman et al. 1982; Southwood 1987). Such communities tend to promote high densities and diversity of organisms (Usher 1976). Rahel (1990) suggested that unstable, varying communities are better suited for examining disturbances caused by abiotic changes. However, in some long-term studies, e.g. impacts of acid rain on forest ecosystems, changes from external agents can be confounded with those resulting from natural succession since they occur simultaneously. Stable habitats, such as stumps, have the advantage of enabling the separation of subtle, time-induced changes brought about by abiotic factors from those effected by natural phenomena, including plant succession.

#### *Collembola and early stages of forest succession*

The old-growth forest is here considered the reference sere (or control), against which the species composition of the other successional seres are compared. In this section and the following one (Collembola in late stages of forest succession), the term "succession" is restricted to the temporal development of the forest sere and not, for example, to changes in the Collembolan fauna of the various decay stages of stumps within a sere. Apart from the depauperated collembolan community of decay stage I stumps, no clear indication of succession was observed in the latter.

The collembolan fauna of the earliest successional sere after disturbance (REG or clear-cut) clearly differed both qualitatively and quantitatively from the typical old-growth forest. This was unexpected because there is evidence that the Collembola as a group was relatively insensitive to clear-cutting, compared to other silvicultural practices (Huhta 1976; Seastedt & Crossley 1981). In our study, many factors were probably responsible for the decline of Collembola in stumps of the REG sere as opposed to the forested seres. These stumps will be more exposed to direct radiation than the soil surface after the canopy has been removed by cutting the old-growth forest. Cutting remains (slash) can effectively insulate the soil surface from extensive heat during the summer months, and retain or even increase the moisture content of the top soil (Huhta 1976). However, our REG seres were slash-burned before planting and this would have diminished the litter and soil collembolan population (Huhta et al. 1969; Vlug & Borden 1973), thereby reducing collembolan inoculum for stumps. Furthermore, extremely high temperatures ( $> 60^{\circ}\text{C}$ ) develop on the soil surface of clear-cuts compared to forested sites (Hungerford & Babbitt 1987), with air temperatures registering about  $30^{\circ}\text{C}$  during August in coastal British Columbia in clear-cuts (Ballard et al. 1977). Judging from Savely's (1939) and Wallace's (1953) data, the interior of stumps in our clear-cuts could have experienced temperatures near  $40^{\circ}\text{C}$ , which have been reported to be harmful to many microarthropods (Woodring & Cook 1962; Madge 1965). Although thermophilic species might withstand higher temperatures, juvenile Collembola are more sensitive and the absolute lethal temperature for most adult Collembola range from  $40$  to  $45^{\circ}\text{C}$  (Christiansen 1964; Thibaud 1977a, b). The survival of some collembolan species in stumps in the REG seres might be related to their capability to migrate away from places with lethal temperatures and the ability of stumps to cool through water loss.

The altered species composition in the REG stumps as compared to OLG and other forested seres reflected the direct impact of clear-cutting and slash-burning. Differential mortality was not the only factor that could cause differences between the seres. Some other subtle biological responses to the disturbance also occurred. The high density and frequency of the isotomid, *Anurophorus septentrionalis*, in the REG seres more than 5 years after disturbance may indicate some extreme microclimatological changes in the REG sere. Although a common and abundant species in Swedish coniferous forests (Bödvarsson

1984), *A. septentrionalis* appears to be a representative of open and dry habitats in North America (Maynard 1951) and may possess a competitive advantage over other species in clear-cut areas. There is no indication that this species, with a reduced furcula, would re-invade the REG sere faster than other species. The ecology of other species in the Pacific Northwest of North America is too poorly known to draw any further conclusions. Since many collembolan species feed on fungi, it might be assumed that changes in their species composition during forest succession are also related to stump microfloral population, which can differ in stumps of open versus forested areas (Savely 1939; Wallace 1953).

#### *Collembola and later stages of forest succession*

Although the seral communities at each site are situated close to each other, within a radius of 1.5 km, and the absence of barriers allowed for free dispersal of the fauna, the ordination analysis (Fig. 3) nevertheless showed some evidence that the collembolan fauna of the whole study area tended to be grouped according to the successional stage (or age) of the forest. The stump fauna of the immature and mature forests seemed to be rather similar, differing only slightly from that of the old growth. The arrangement of this classification along the abscissa (Fig. 3, Axis 1) followed the order of succession of the forests of which the stumps with their fauna are a part. Since no qualitative or quantitative seasonal changes of the stump fauna were observed in the seres, it was not obvious that differences in abiotic conditions alone (for example, temperature and moisture) brought about the "biotic" differences observed in the seres. A combination of biotic and abiotic attributes of the ecosystem surrounding the stumps is likely to have determined the composition of the stump fauna. Sere is a major factor when considered on an extended spatio-temporal scale, but the stump itself becomes important when handled within a season (Setälä et al. 1994). Once disturbed, it took at least 40 years, but more likely 100 years, for the *Collembola* fauna to return to the state that prevailed before the perturbation.

There was an indication that rarer species became fewer with forests succession. The OLG seres are stable environments where established biological interactions prevail. In these situations, it is more difficult for new or rarer species to enter the already saturated environment. Conversely, in the REG seres all niches are not occupied and new comers, especially opportunistic r-strategists, are able to establish themselves.

#### *Collembola and stump decomposition*

*Collembola* are not known to burrow into wood, but are often associated with coarse woody debris (Snider 1994). They are able to feed on a wide range of substances expected in decaying stumps. Potential foods include decaying plant material, bacteria, faeces, carrion and living prey (Wallwork 1970). Although woody and other hard plant materials comprise a small portion of the diet of most *Collembola*, they nevertheless consume such materials (Davis & Harris 1936; Poole 1959; Marshall 1978; Muraleedharan and Prabhoo 1978). Therefore, *Collembola* could promote the decomposition of stumps directly by their feeding on the woody material and indirectly through consumption of primary decomposers (bacteria and fungi) as has been demonstrated for soil species (Rusek 1986). In addition, the increased surface area resulting from the conversion of woody substrate to faecal pellets, especially by *Folsomia* sp. ? *macroseta*, provides a new and suitable substrate for microbial colonization (Parkinson 1988). An average of 120 collembolans present in a volume of 150 cm<sup>3</sup> (or 18 individuals per g of dry wood) of decaying stump undoubtedly exerts a significant influence on the fungal and bacterial populations of stumps.



## Conclusions

Until the roles of all stump-fauna groups have been established, it is not possible to determine the full contribution of the collembolan fauna to stump decomposition, or to consider specific modifications in silvicultural practices that will mitigate against loss of this fauna. However, it should be recognized that stumps harbour a species-rich and numerically abundant collembolan fauna that approximates diversity and abundance in soil. This stump collembolan community is apparently stable and represents a specialized microhabitat for *Collembola* in Pacific Coast forests. Stumps therefore provide an important buffer against disturbances following clear-cuts. There is a great need for similar studies of other forest ecosystems to evaluate how forestry practices, especially whole-tree logging and de-stumping, will affect stump fauna. At least 40 years will be required after clear-cutting before the collembolan populations in some regenerated sites take on the characteristics of old growth forests, a period not unlike the 30 years required for spiders in the H. J. Andrews Experimental Forest, Washington State, USA, to reach a similar equilibrium (McIver et al. 1992). Where many plant successional stages are close together, as in this study, collembolan recovery seems possible within a rotational period in coastal Douglas-fir forests (about 80 years). A longer period than 40 years, however, might be required for collembolan recovery in larger clear-cut sites and in other forest types.

## Acknowledgements

We thank the Finnish Academy of Sciences for supporting one of us (H. S.) with an overseas postdoctoral stipend. T. Bown, G. Lait and K. McCullough, Pacific Forestry Centre, Victoria, British Columbia, provided technical assistance for which we are grateful.

**Appendix.** Summary of collembolan species. AB. = Abundance: total number of individuals collected from all samples and seasons per sere (REG = Regeneration; IMM = Immature; MAT = Mature; OLG = Old growth). FR. = Frequency %: number of records for all samples

	REG		IMM		MAT		OLG		Sites		
	AB.	FR.	AB.	FR.	AB.	FR.	AB.	FR.	1	2	3
<b>Family HYPOGASTRURIDAE Börner, 1913</b>											
<i>Ceratophysella</i> sp.	22	7	4	11	6	17	2	6	6	2	26
<i>Hypogastrura nivicola</i> (Fitch, 1846)	0	0	58	22	0	0	0	0	54	0	4
<i>Hypogastrura purpurescens</i> (Lubbock, 1868)	84	19	12	17	8	1	14	33	2	64	52
<i>Hypogastrura tullbergi</i> (Schäffer, 1900)	0	0	42	11	20	28	0	0	0	52	10
<i>Mitchellania californica</i> (Bacon, 1914)	0	0	0	0	0	0	2	6	0	1	1
<i>Mitchellania virga</i> Christiansen and Bellinger, 1980	0	0	4	6	0	0	4	6	4	3	1
<i>Mitchellania vulgaris</i> Yosii, 1960	6	7	2	6	8	11	0	0	12	2	2
<i>Mitchellania</i> sp.	0	0	4	6	0	0	4	11	6	2	0
<i>Schaefferia cheoha</i> Wray, 1963	0	0	0	0	2	6	0	0	2	0	0
<i>Willemia denisi</i> Mills, 1932	4	3	12	17	28	28	16	33	16	34	10
<i>Xenylla humicola</i> (O. Fabricius, 1870)	2	3	2	6	0	0	0	0	0	0	4



## Appendix. (Continued)

	REG		IMM		MAT		OLG		Sites		
	AB.	FR.	AB.	FR.	AB.	FR.	AB.	FR.	1	2	3
<b>Family ONYCHIURIDAE Börner, 1913</b>											
<i>Hymenaphorura cocklei</i> (Folsom, 1908)	100	33	100	33	30	39	276	72	316	136	54
<i>Hymenaphorura subtenuis</i> (Folsom, 1917)	38	11	6	617	104	22	14	17	42	8	112
<i>Hymenaphorura</i> sp. ? <i>talus</i> Christiansen and Bellinger, 1981	36	22	256	67	240	61	216	67	12	280	456
<i>Lophognathella choreutes</i> Börner, 1908	0	0	4	11	48	17	0	0	2	6	44
<i>Mesaphorura macrochaeta</i> Rusek, 1976	2	6	0	3	0	6	0	0	0	2	0
<i>Mesaphorura pacifica</i> Rusek, 1976	0	0	0	0	2	1	2	6	2	2	0
<i>Mesaphorura yosiii</i> Rusek, 1967	720	63	982	100	1110	100	1122	100	1014	1697	1223
<i>Mesaphorura</i> sp.	118	22	94	11	102	28	4	6	142	118	58
<i>Onychiurus</i> sp. ? <i>lusus</i> Christiansen and Bellinger, 1981	2	4	0	0	0	0	18	22	18	2	0
<i>Onychiurus</i> sp.	16	11	44	11	26	11	66	28	20	84	48
<i>Paronychiurus flavescens</i> (Kinoshita, 1916)	0	0	112	28	38	17	32	28	22	160	0
<b>Family ANURIDIDAE Stach, 1949</b>											
<i>Friesia millsi</i> Christiansen and Bellinger, 1973	18	19	108	56	114	56	94	61	50	142	142
<i>Friesia quinta</i> Christiansen and Bellinger, 1973	12	6	10	11	48	28	44	44	32	50	32
<i>Morulodes serratus</i> (Folsom, 1916)	4	7	4	11	6	17	8	22	7	7	8
<b>Family BRACHYSTOMELLIDAE Stach, 1949</b>											
<i>Odontella cornifer</i> Mills, 1934	18	22	50	39	32	39	18	33	32	28	58
<i>Odontella shasta</i> Christiansen and Bellinger, 1980	0	0	4	11	0	0	1	6	5	0	0
<i>Odontella substriata</i> Wray, 1952	12	7	0	0	58	17	1	6	3	68	0
<i>Xenyllodes armata</i> Axelson, 1903	0	0	0	0	10	6	0	0	0	10	0
<b>Family NEANURIDAE Salmon, 1964</b>											
<i>Micranurida spirillifera</i> Hammer, 1953	12	22	82	78	104	72	66	72	60	84	120
<i>Paranura colorata</i> Mills, 1934	12	15	12	28	18	39	12	22	28	16	10
<i>Pseudachorutes aureofasciatus</i> (Harvey, 1898)	0	0	0	0	4	11	0	0	0	4	0
<i>Pseudachorutes corticicolus</i> (Schäffer, 1896)	16	26	4	18	14	22	4	11	26	10	14
<i>Pseudachorutes lunatus</i> Folsom, 1916	0	0	1	6	0	0	0	0	2	0	0
<i>Pseudachorutes saxatilis</i> MacNamara, 1920	0	0	0	0	0	0	4	2	4	0	0
<b>Family ENTOMOBRYIDAE Tomosvary, 1882</b>											
<i>Entomobrya triangularis</i> Schött, 1896	12	19	18	39	20	44	18	50	18	24	26
<i>Entomobrya</i> sp. 1	7	19	4	11	2	6	12	22	8	17	0
<i>Entomobrya</i> sp. 2	2	3	2	6	0	0	0	0	4	0	0

## Appendix. (Continued)

	REG		IMM		MAT		OLG		Sites		
	AB.	FR.	AB.	FR.	AB.	FR.	AB.	FR.	1	2	3
<i>Pseudosinella collina</i> Wray, 1952	8	15	4	11	2	6	2	6	3	12	1
<i>Sinella baca</i> Christiansen and Bellinger, 1980	2	3	4	11	4	11	6	11	8	4	4
<i>Sinella bioculata</i> (Schött, 1896)	0	0	0	0	2	6	0	0	0	2	0
<b>Family ISOTOMIDAE Schaffer, 1896</b>											
<i>Anurophorus septentrionalis</i> Palissa, 1966	282	80	28	28	10	22	18	39	68	90	180
<i>Ballistura libra</i> Christiansen and Bellinger, 1980	168	37	22	11	70	27	42	11	122	152	28
<i>Cheirotona</i> sp.	0	0	0	0	2	6	0	0	2	0	0
<i>Coloburella octogenaria</i> (Mills and Schmidt, 1957)	8	3	0	0	0	0	8	6	8	8	0
<i>Desoria alaskensis</i> (Fjellberg 1978)	0	0	0	0	0	0	5	6	5	0	0
<i>Desoria ekmani</i> (Fjellberg, 1977)	4	6	4	11	4	11	2	6	6	0	8
<i>Desoria flora</i> Christiansen and Bellinger, 1980	4	3	0	0	0	0	0	0	4	0	0
<i>Desoria notabilis</i> (Schaffer, 1896)	4	6	156	67	34	33	36	28	36	120	74
<i>Desoria uniens</i> Christiansen and Bellinger, 1980	2	3	4	11	4	6	0	0	6	2	2
<i>Folsomia</i> sp. nr. <i>bisetosa</i> Gisin, 1953	2	22	10	2	58	39	34	22	52	24	28
<i>Folsomia duodecimoculata</i> Ford, 1962	0	0	0	0	2	6	0	0	0	2	0
<i>Folsomia</i> sp. ? <i>macroseta</i> Ford, 1962	204	63	1722	100	1634	100	1260	94	1114	1700	2006
<i>Folsomia nivalis</i> Packard, 1873	2	3	18	17	76	28	26	33	30	28	64
<i>Folsomia stella</i> Christiansen and Tucker, 1977	0	0	2	6	84	33	44	33	78	16	36
<i>Isotoma</i> sp.	4	3	2	6	0	0	2	6	5	1	2
<i>Metisotoma grandiceps</i> (Reuter, 1891)	2	3	0	0	2	6	2	6	1	3	2
<i>Micrisotoma achromata</i> Bellinger, 1952	40	33	0	0	30	39	18	28	14	37	37
<i>Proisotoma beta</i> Christiansen and Bellinger, 1980	0	0	0	0	14	17	2	6	16	0	0
<i>Pseudisotoma monochaeta</i> Kos, 1942	0	0	4	11	28	28	14	11	12	4	30
<i>Pseudisotoma sensibilis</i> (Tullberg, 1876)	68	52	128	72	96	61	238	89	147	149	234
<i>Tetracanthella pacifica</i> Rusek and Marshall, 1976	122	22	0	0	12	17	36	22	46	120	4
<i>Vertagopus alpa</i> Christiansen and Bellinger, 1980	8	7	62	11	52	28	58	22	114	54	12
<i>Vertagopus arborea</i> (Linnaeus, 1758)	2	3	6	17	6	11	0	0	2	6	6

## Appendix. (Continued)

	REG		IMM		MAT		OLG		Sites		
	AB.	FR.	AB.	FR.	AB.	FR.	AB.	FR.	1	2	3
<b>Family TOMOCERIDAE</b> Schäffer, 1896											
<i>Pogonognathellus flavescens</i> (Tullberg, 1871)	12	19	28	78	40	50	50	67	22	70	38
<i>Pogonognathellus</i> sp.	46	48	100	61	78	56	32	44	70	94	92
<i>Plutomurus brevimucronatus</i> (Denis, 1929)	0	0	34	39	4	11	18	28	16	18	22
<i>Plutomurus wilkeyi</i> (Christiansen, 1965)	0	0	4	6	0	0	22	17	12	10	4
<b>Family ARRhopALITIDAE</b> Stach, 1956											
<i>Arrhopalites hirtus</i> Christiansen, 1966	7	7	18	39	26	50	8	22	30	11	18
<b>Family KATIANNIDAE</b> Börner, 1913											
<i>Sminthurinus conchyliatus</i> Snider, 1978	10	19	88	72	26	39	46	56	38	56	76
<b>Family DICYRTOMIDAE</b> Börner, 1906											
<i>Ptenothrix maculosa</i> (Schött, 1891)	2	6	0	0	28	39	0	0	22	6	2
<b>Family NEELIDAE</b> Folsom, 1896											
<i>Megalothorax minimus</i> Willem, 1900	18	19	24	44	26	33	18	22	44	34	8
Total	4124 5948 5529										

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